9 Climate Change and Alien Species in South Africa

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Abstract

South Africa has a long history of human-mediated introductions of species from all major taxonomic groups. Close to 9000 alien terrestrial plant species have been introduced, and all of the country's biomes have already been invaded. Invasive species are threatening the country's ecosystems in numerous ways, but the effect of climate change on these invasions is predicted to be complex and cascading and remains poorly understood. The relationship between climate and invasive species biology is well established, and there is no question that climate change will influence the ecology of invasive species significantly. If left unmanaged, these effects are expected to increase substantially. Besides terrestrial plants, numerous animals have also invaded the country's landscapes. South Africa's freshwater ecosystems have been invaded by both alien as well as extralimital introductions (indigenous species outside their historical extent of occurrence). The status of invasion in the marine environment remains poorly studied, and knowledge of the status of invasions and predictions regarding the impacts of climate change remain largely speculative. This chapter highlights the current status of invasions in South Africa and discusses some of the direct and indirect effects climate change is likely to have on these invasions.

Dedication

We dedicate this chapter to the memory of Phil Hockey, who had an enduring interest in avian range expansions and has made their study so much more straightforward through his significant contributions to ornithology.

Introduction

South Africa covers 1.22 million km^2, about 2% of the world's surface area, and has a coastline of about 2800 km. The country has a warm, temperate climate and is mostly arid, with large parts receiving less than 500 mm rainfall annually, especially the west, which is drier than the east (Fig. 9.1) (O'Brien, 1998; van Rensburg *et al*., 2002). Nine major biomes (Desert, Succulent Karoo, Nama-Karoo, Fynbos, Albany Thicket, Grassland, Savannah, Forest and Indian Ocean Coastal Belt), each with distinct bioclimatic regimes, characterize the country (Mucina and Rutherford, 2006), which also includes three biodiversity hotspots (Cape Floristic Region, Maputaland–Pondoland–Albany and the Succulent Karoo). It is home to about 10% of the world's plant species, 13% of bird and mammals and 23% of marine inhabitants, with high levels of endemism in all groups (DEAT, 1997; EWT, 2002). South Africa also governs the Prince

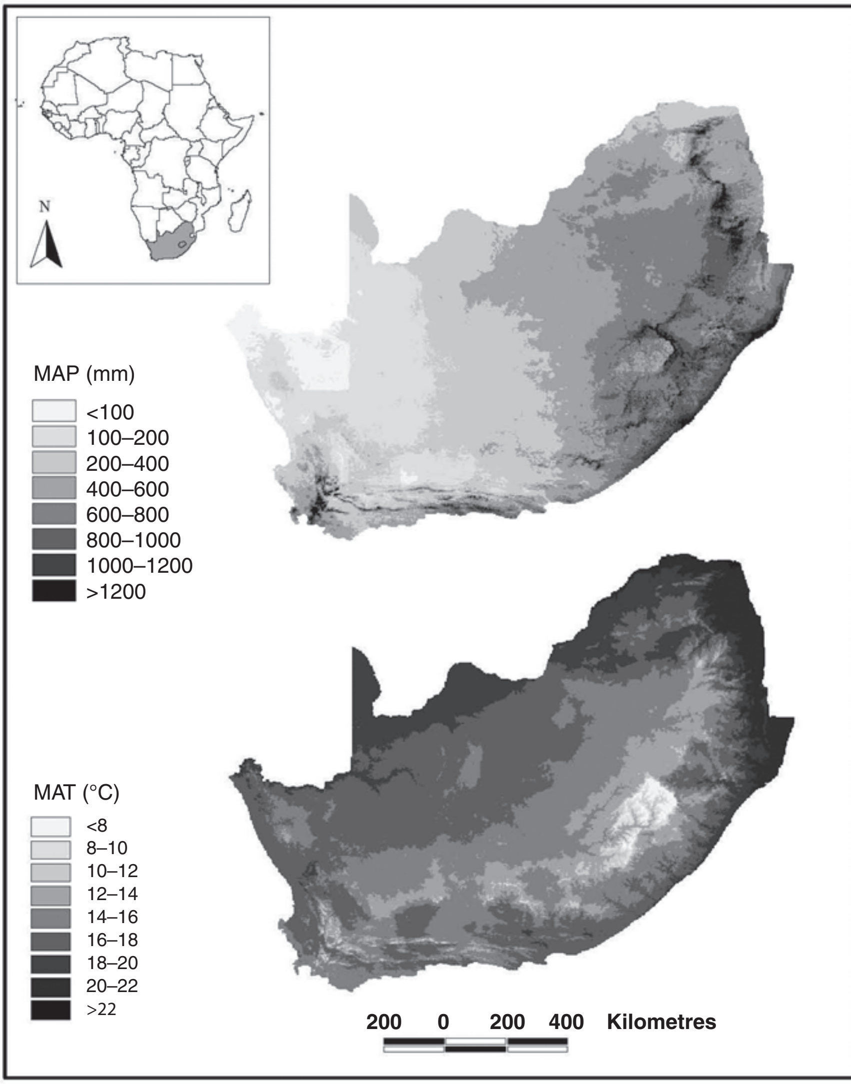

Fig. 9.1. Mean annual temperature (MAT) and precipitation (MAP) for South Africa. Data from the *South African Atlas of Agrohydrology and Climatology* (Schulze *et al*., 1997; interpolated 1′ × 1′ data).

Edward Island archipelago in the sub-Antarctic, which lies approximately 1770 km south-east of Port Elizabeth, South Africa, and has a cool, moist climate characterized by two major biomes (Tundra and Polar Desert) and many distinct habitat types (Chown and Froneman, 2008).

South Africa has a long history of human-mediated introductions of organisms from all the major taxonomic groups (Richardson *et al*., 2003). Cattle, sheep, goats, dogs and burweed were introduced approximately 2000 years ago as humans migrated southwards, but the arrival of European settlers in the mid-17th century led to a large increase in introductions (Macdonald *et al*., 1986a). At present, all biomes are invaded, with the highest density of alien species occurring in the eastern parts of the country (Rouget *et al*., 2004; Richardson *et al*., 2005; Chown and Froneman, 2008; Spear and Chown, 2009). The prominence of alien trees and shrubs as major invaders of terrestrial systems is an unusual feature of South Africa's invasive biota; grasses and other herbaceous species dominate invasive floras in most other parts of the world (Richardson *et al*., 1997).

Approximately 8750 alien terrestrial plant species from all growth forms are known to be present, and at least 180 of these are currently invasive (Table 9.1; Richardson *et al*., 2011). At least 771 species of alien trees have been introduced to South Africa (von Breitenbach, 1990). The diversity of bioclimates in South Africa provides niches for species from tropical, temperate and Mediterranean climate regions. Most invasive alien plants from tropical regions are South American, while northern temperate species have originated mostly from Europe or Asia. Australia has

Table 9.1. Current estimates of the number of alien and invasive species (*sensu* Pyšek *et al*., 2004) in South African terrestrial and aquatic habitats.

	Number of alien species	Number of invasive species	Sources
Terrestrial			
Plants[a]	8750	199	Macdonald *et al*., 2003; Richardson *et al*., 2011
Mammals	50	10	Richardson *et al*., 2011
Birds	77	7	Dean, 2000; van Rensburg *et al*., 2011
Reptiles	275	0	van Wilgen *et al*., 2010
Amphibians	14	0	van Rensburg *et al*., 2011; N.J. van Wilgen, Stellenbosch, 2010 personal communication
Arthropods[b]	305	Unknown	Lach *et al*., 2002; Macdonald *et al*., 2003
Molluscs	34	10	Herbert, 2010
Microbes	Unknown	Unknown	Pimentel *et al*., 2001
Freshwater			
Plants	23	13	Hill, 2003; Macdonald *et al*., 2003
Fish (freshwater)[c]	58	37	Macdonald *et al*., 2003
Crayfish	4	4	de Moor, 2002
Molluscs	10	4	Appleton, 2003
Fish parasites/ diseases	8	8	Macdonald *et al*., 2003
Marine[d]			
Plants/algae	6 (4)		Mead *et al*., 2011
Crustaceans	22 (11)	2	Mead *et al*., 2011
Insects	1		Mead *et al*., 2011
Molluscs	12 (9)	1	Mead *et al*., 2011
Fish	1		Mead *et al*., 2011
Other	43 (15)	1	Mead *et al*., 2011

Notes: [a]At least 771 tree species have been introduced to South Africa over the past 300 years (von Breitenbach, 1990); [b]numerous insect species were introduced as biocontrol agents; [c]33 extraregional (species from outside South Africa) and 25 extralimital (indigenous species outside their historical extent of occurrence); [d]number of cryptogenic species (species of unknown origin) in brackets.

been the largest contributor of southern temperate invasive plant species (Henderson, 2006). The most important aquatic weeds are from tropical South America (Henderson, 2006; Coetzee *et al*., 2011). Many terrestrial invertebrate species have been introduced and have become invasive, including several that are pests of agriculture and which have substantial impacts on biodiversity, such as the Argentine ant, *Linepithema humile* (Annecke and Moran, 1982; Bond and Slingsby, 1984; Herbert, 2010).

Aquatic invertebrate invaders have not been well studied, but several molluscs are important, including *Aplexa marmorata*, *Lymnaea columella*, *Physa acuta* and *Tarebia granifera*, which are established in the freshwater ecosystems of the Kruger National Park (de Kock and Wolmarans, 2008). Alien freshwater fish have originated from South African river systems through inter-basin transfers (extralimital introductions; approximately 25 species) as well as extraregional introductions (species from outside South Africa; 33 species) (Table 9.1; Macdonald *et al*., 2003).

In contrast to terrestrial plant invasions, far fewer terrestrial vertebrates have invaded South African ecosystems, and no extraregional amphibian or reptile species are currently considered invasive, although several species are established (van Wilgen *et al*., 2008a; van Rensburg *et al*., 2011). Few bird species have invaded, and those that have are commensals (Table 9.1; Dean, 2000). Among the mammals, commensal rodent species which pose substantial human health risks through their vector status are in a state of dynamic change: a recently discovered introduction, *Rattus tanezumi*, is widespread (Taylor *et al*., 2008). Many indigenous mammal species have been moved intentionally outside of their historical ranges in South Africa. Such extralimital introductions have led to homogenization of the fauna (Spear and Chown, 2008, 2009). Species have also been introduced from outside South Africa (extraregional introductions) and, after the USA, South Africa is home to more alien ungulate species than any other country.

Assessing the Influence of Climate Change on Invasive Species

The impacts of invasive species on South African ecosystem services, biodiversity and the economy are multifaceted. Although these have not been quantified comprehensively, some countrywide assessments have been made, looking at all major taxonomic groups (van Wilgen *et al*., 2001; Pimentel, 2002; van Wilgen and Richardson, 2009; van Rensburg *et al*., 2011). The effect of climate change on these invasions is little understood. However, the extensive research conducted on invasive species elsewhere does enable several informed predictions regarding the possible impact and effect of climate change on invasive species to be made.

Direct effects

The most direct effect of a changing climate on invasive species will be through changes to distribution and life history as a consequence of altered patterns of precipitation and temperature and the increased frequency of extreme events, such as floods and droughts (Hobbs and Mooney, 2005). Kruger and Sekele (2012) found that since the 1960s, warm extreme temperatures have increased, while cold extreme temperatures have decreased, and this pattern has been observed across the country. For South Africa's interior, annual mean temperatures are expected to increase by 2.5–3.5°C by 2050, while the coastal regions could experience temperature increases of up to 2°C (Knoesen *et al*., 2009). The increase in temperature will be accompanied by increased evaporation and the east to west rainfall gradient (Fig. 9.1) is likely to be exacerbated. A recent study investigated the precipitation trends over the past century and found no evidence of changes in rainfall patterns for large parts of the country, while only some areas showed increases or decreases in precipitation trends (Kruger, 2006). However, it is predicted that by 2100 the largest part of the country could experience increased rainfall, with only the west coast (Succulent Karoo and the western parts of the Fynbos biome) predicted to become more arid (Knoesen *et al*., 2009). Projected rainfall anomalies include floods, which show no clear pattern, and short droughts, which are expected to decrease in frequency; current patterns of longer duration droughts are unlikely to change (Knoesen *et al*., 2009). These direct effects of climate change are likely to drive substantial changes to the geographic ranges of both indigenous and alien species (Richardson *et al*., 2000; Erasmus *et al*., 2002; Rouget *et al*., 2004; Huntley and Barnard, 2012). The range shift of species due to climate change is expected to be similar to natural dispersal, with leading edge range shifts, but long-distance dispersal and movement via corridors also needs to be considered (Tolley *et al*., 2008; Wilson *et al*., 2009). This is likely to be more important for alien species, especially those that are frequently dispersed by humans (Trakhtenbrot *et al*., 2005). Following the changes in rainfall patterns, more alien species may appear in the eastern parts of the country (i.e. tropical species) than in the western arid parts (Rouget *et al*., 2004).

Assessments of the effects of climate change on indigenous and invasive biota must also consider changes in ecosystem function that alter invasibility. For example, changes in the frequency and intensity of extreme events such as storms, fires, droughts and floods have the potential to increase ecosystem susceptibility to invasion (Hobbs and Mooney, 2005). Changing precipitation and rainfall regimes may also alter the demographic distribution of C_3 and C_4 plants, which will drive crucial changes in fire regimes (Wigley *et al*., 2010; Higgins and Scheiter, 2012). Increases in carbon dioxide concentration ([CO_2]) are likely to have major effects on tree–grass dynamics in grasslands and savannahs, because of the different photosynthetic pathways used by the different growth forms. Differential responses of plant species to increased atmospheric [CO_2] may be driving the expansion and densification of indigenous trees in South African grasslands (Bond and Midgley, 2012) and may alter the relative abundance of C_3 and C_4 plants radically in different biomes. This has profound implications for ecosystem functioning and invasibility (Richardson *et al*., 2000), and such interactions are likely to cause a substantial reshuffling of invasive species in South Africa.

Indirect effects

Climate change will also affect introduced species indirectly by influencing the nature and intensity of human activities. Biological invasions are closely linked to human activities, particularly trade and the disturbance of natural ecosystems through changes in land use (Le Maitre *et al*., 2004; Richardson *et al*., 2005; Thuiller *et al*., 2007; King and Tschinkel, 2008). The intentional introduction of species for human activities associated with recreation (fishing – Shelton *et al*., 2008; hunting – Spear and Chown, 2009), the pet trade (van Wilgen *et al*., 2010) and agriculture (forestry – Richardson, 1998; agriculture and horticulture – Le Maitre *et al*., 2004) have contributed significantly to invasive species introductions. As humans adapt to novel climatic conditions, the donor and recipient regions of pathways, as well as the intensity with which these are used, may change (Galil *et al*., 2007).

Changes in land use associated with increased urbanization and economic and infrastructure development are also likely to result in new dispersal corridors (e.g. roadside verges) for invasive species (Kalwij *et al*., 2008). The intensification of land use may also increase nutrient deposition (e.g. nitrogen, phosphorus) in soil and water, enhancing invasion vulnerability (Richardson *et al*., 2000; Coetzee *et al*., 2009). Human settlements adjacent to protected areas may serve as sources of propagules of alien species, as well as drivers of disturbance that render areas inside protected areas more susceptible to invasion (Alston and Richardson, 2006; Foxcroft *et al*., 2011; Jarošík *et al*., 2011). Furthermore, in an attempt to curb climate change, carbon sequestration projects are being implemented, often in the form of plantations of fast-growing alien trees such as *Pinus* and *Eucalyptus* (Christie and Scholes, 1995), trees that have escaped the plantations and are invading the South African landscape. However, some sequestration projects are focusing on rehabilitating degraded rangelands using indigenous species. Such projects should be supported, as carbon storage in the long term has been found to be greater using indigenous than alien species (van Rooyen *et al*., 2013). As climate change alters human activities, many introduced species may become 'change passengers', with greater exposure to new regions. Overall, human-mediated dispersal of invasive species is well recognized (Trakhtenbrot *et al*., 2005), and the indirect effects of climate change as outlined above are likely to play a significant role in driving further invasions in South Africa.

A Synopsis of the Current Status of Invasion and the Predicted Effect of Climate Change on Invasive Species

Terrestrial

Current status

Invasive plant species now cover about 8%, or 10 million hectares (Mha), of South Africa's surface area (Le Maitre *et al*., 2011), equating to approximately 1.813 million condensed hectares, calculated as the percentage invasion (density) as a proportion times the area of the polygon (Marais and Wannenburgh, 2008; van Wilgen *et al*., 2012). Plant invaders pose a significant threat to South African biodiversity: they have already been implicated in the extinction of at least 58 plant species in the Cape Floristic Region and are threatening thousands more (Macdonald *et al*., 2003; Gaertner *et al*., 2009). Invasive plants are also negatively affecting other groups, such as birds (Allan *et al*., 1997; Dean *et al*., 2002) and several invertebrate groups (grasshoppers – Samways and Moore, 1991; ground-living invertebrates – Samways *et al*., 1996; dung beetles – Steenkamp and Chown, 1996; spiders – van der Merwe *et al*., 1996; dragonflies and damselflies – Samways and Taylor, 2004; Samways *et al*., 2005).

Plant invasions also have a significant impact on South Africa's water resources. An estimated 7% of mean annual runoff is currently used by invasive plants, with an annual total of US$773 million in water-related losses (Le Maitre *et al*., 2011). Invasive plants currently reduce the grazing potential by *c*.123,000 large livestock units, with an estimated unit-price estimate of US$329.47 per large livestock unit (Le Maitre *et al*., 2011). If invasive species continue to spread and degrade grasslands, grazing potential could be reduced by up to 70% (van Wilgen *et al*., 2008b). The cost of clearing invasive plant species across the country has been estimated at approximately US$1.2 billion (Pimentel, 2002). Currently, the Working for Water programme and a provincial programme in KwaZulu-Natal spend *c*.US$80 million per annum on the clearing and management of alien species. An estimated 42% of South Africa's arthropod agricultural pests are alien species which cause crop losses and impact food security to the value of approximately US$1 billion per annum, with alien weeds and pathogens adding a further US$3.3 billion in crop losses annually (Pimentel *et al*., 2001). For South Africa alone, the total cost of invasive alien plant species has been estimated to be between US$867 million (Le Maitre *et al*., 2011) and US$1 billion annually (Pimentel *et al*., 2001). Many introduced species bring substantial economic benefits, but the environmental impacts of some of these species result in complex conflicts of interest. Considerable attention is being given to formulating trade-offs to resolve such conflicts; for example, in the case of forestry trees that also cause major problems as invasive species (van Wilgen *et al*., 2011; van Wilgen and Richardson, 2012).

At least 50 mammal species have been introduced to South Africa, many intentionally for pest control, pets, food or as the source of other animal products, as well as for hunting and ornamental purposes (Table 9.1; van Rensburg *et al*., 2011). In addition to domestic animals, such as goats, sheep and cattle, 38 ungulate species have also been introduced or translocated within the country, largely for the game ranching and hunting industries (Spear and Chown, 2009). At least 77 bird species have been introduced to South Africa, but only a few commensal species have established successfully (Table 9.1; Dean, 2000; van Rensburg *et al*., 2011). Approximately 275 species of reptiles and at least 14 species of amphibians have been introduced to South Africa, mainly through the pet trade (van Wilgen *et al*., 2010; N.J. van Wilgen, Stellenbosch, 2010, personal communication). Although some alien reptile species have established feral populations, none are currently invasive (Richardson *et al*., 2011; van Rensburg *et al*., 2011). Three amphibian species have established extralimital populations in the Western Cape and are invading (Measey and Davies, 2011). South African ecosystems appear resistant to invasion by extraregional alien amphibians and reptiles, but this may be an artefact of low propagule pressure and the short residence time of these species. Increasing rates of introduction and changing environmental conditions may well render ecosystems more susceptible to invasion.

Data on alien invertebrates in South Africa are limited. At least 24 alien spider species have been recorded (Macdonald *et al*., 2003). Of the 34 mollusc species known to have been introduced, 28 are established and 10 of these are invasive (Table 9.1; Herbert, 2010). Of the 40 top crop pests in South Africa, about 17 species are alien (Pimentel, 2002). Some insect invaders with potentially detrimental effects on biodiversity include the varroa mite (*Varroa destructor*) and the Argentine ant (*L. humile*; Lach *et al*., 2002). While not invasive, over 225 insect species have been introduced as biological control agents against insect pests and a further 56 species to control weeds (Lach *et al*., 2002; Macdonald *et al*., 2003; Klein, 2011). Little information is available on the status of alien microbes (viruses, bacteria, most fungi and most single-celled organisms) or their impact on the environment, human health and the economy (Table 9.1; Pimentel *et al*., 2001).

Predictions

South Africa is expected to be affected significantly by climate change over the next few decades. Mean annual temperatures are expected to rise by 2.5–3.5°C by 2050 (Knoesen *et al*., 2009). Large parts of the country are expected to experience more extreme rainfall events, which are likely to lead to the increased frequency as well as severity of floods. Predictions suggest an increase in shorter (1- to 2-year) droughts, whereas no change is predicted in longer (3 consecutive years or longer) drought events (Knoesen *et al*., 2009). Raised levels of atmospheric [CO_2] have been shown to increase photosynthesis, plant water-use efficiency and biomass in many plant species (Bazzaz, 1990; Ziska, 2003), and both indigenous and alien woody plants will benefit from this CO_2 enrichment (Bond and Midgley, 2012; Higgins and Scheiter, 2012). The increased growth rate of woody species and their enhanced ability to survive fires is likely to drive a marked increase in the invasion of grasslands by woody plants, as is being observed with the range expansion of *Prosopis* species in North America (Polley *et al*., 2002). Through this increased plant growth, the carbon:nitrogen ratio in the leaves may be modified, resulting in nitrogen becoming the limiting nutrient for herbivorous insects. Such altered plant–herbivore interactions could result in increased leaf herbivory and decreased insect growth, but ecosystem effects are variable (Coviella and Trumble, 1999; Lindroth, 2010). One consequence of rising CO_2 may well be a reduced ability of crop species to resist invasive herbivores (Zavala *et al*., 2008), though such interactions have not been explored for the region. In the mesic parts of South Africa, increased water-use efficiency resulting from increased atmospheric [CO_2] could contribute to flooding events due to waterlogged soil, while in arid areas it could open up niches for alien species that require more water (Smith *et al*., 2000; Betts *et al*., 2007; but see Piao *et al*., 2007).

The response of the *Prosopis* species complex to climatic factors in South Africa has been examined using bioclimatic modelling and by inferring the processes that have driven range changes in different parts of the invasive range (Richardson *et al*., 2000). *Prosopis* has invaded the arid and semi-arid areas of South Africa, covering 19% of the total invaded area, or an estimated 1.8 Mha (Marais and Wannenburgh, 2008), posing a significant threat to biodiversity (Steenkamp and Chown, 1996; Dean *et al*., 2002) and grazing resources (van Wilgen and Richardson, 2009). Warming alone is expected to decrease substantially the suitable area for this species, driving an eastward shift in range (Richardson *et al*., 2000). However, rainfall is predicted to increase across the area currently occupied by *Prosopis*; this could facilitate further spread in all directions, particularly to the currently arid western parts. Decreases in fire frequencies and increased grazing intensity will also alter spread by allowing this taxon to move eastwards and northwards, respectively (Richardson *et al*., 2000).

With increased urbanization and economic development, natural habitats are being transformed to meet the needs of a rapidly growing human population. Changes in urbanization and development associated with land use and land transformation in response to a changing climate are difficult to forecast for South Africa. Propagule pressure of alien species has been found to be closely related to human activities (Lockwood *et al*., 2005). Hence, it is likely that climate-driven changes to the spatial patterns of human activities will affect propagule availability significantly, exposing many new areas to invasion by alien species. In the absence of effective policy implementation, increased demands for goods and services may also therefore lead to heightened pressure from invasive species, as seen elsewhere (see Hulme *et al*., 2008).

Fresh water

Current status

South Africa's freshwater systems have been invaded by at least 58 alien fish species, 33 of which are extraregional introductions and the remaining 25 extralimital transfers (Table 9.1; Richardson *et al*., 2011). At least 37 of these alien species are considered detrimental to the aquatic habitats that they occupy. Predatory invasive fish reduce the abundance of indigenous fish and insects, and may cause local extinctions (Weyl and Lewis, 2006; Lowe *et al*., 2008; Shelton *et al*., 2008). Four freshwater crayfish have established following escape from aquaculture (de Moor, 2002). About ten freshwater gastropod species have been introduced, two of which are invasive and a further two undergoing range expansion (Appleton, 2003). At least eight fish parasites and diseases have also been introduced to South Africa (Macdonald *et al*., 2003). In addition to the aquatic animal invaders, South Africa has also been invaded by at least 21 aquatic and wetland plant species (Table 9.1; Henderson and Cilliers, 2002). These have caused extensive disruption to South Africa's freshwater systems by interrupting water flow, degrading water quality, increasing evapotranspiration and increasing erosion (Le Maitre *et al*., 2011; van Wilgen and de Lange, 2011).

The major pathways of introduction for South African freshwater invaders have been the aquarium trade, aquaculture and introductions of fish for sports and food, while most extralimital introductions are attributable to inter-basin transfers (Macdonald *et al*., 1986a; Richardson *et al*., 2011). The introduction and translocation of organisms often includes the transfer of their parasites, particularly in the case of fish. Furthermore, fish translocations have resulted in hybridization with closely related species; e.g. Nile tilapia (*Oreochromis niloticus*) hybridizes with other tilapia species (van der Waal and Bills, 2000; Canonico *et al*., 2005).

Predictions

Climate change will undoubtedly affect South Africa's aquatic ecosystems through increased temperatures and evaporation and through altered rainfall patterns. Increases in water temperature, together with decreased water flow, have been predicted for southern Africa. This could result in deterioration in water quality, affecting freshwater ecosystems and the utilization of water resources by humans (van Vliet *et al*., 2013). Due to these changes, land use is likely to change in response to the changing climate. Urbanization, human population growth and economic development are increasing the pressure on South Africa's water supplies over much of the country. This will increase the demand for dam construction and inter-basin transfers, which will lead to more transfers of organisms between regions (both species native to South Africa and alien species) (Kolar and Lodge, 2000; Johnson *et al*., 2008). The increased transformation of natural environments for agriculture will alter aquatic systems by increasing the runoff of agricultural effluent into rivers and dams, with impacts on water quality (de Villiers, 2007). The eutrophication of freshwater systems often makes ecosystems less suitable for indigenous species and more suitable for alien species, as eutrophication acts as a disturbance event and some alien species might be better adapted to nutrient-rich environments than indigenous species (Byers, 2002). More intensive agriculture may also alter water temperature (Kolar and Lodge, 2000), which may reduce habitat quality for freshwater species such as dragonflies and damselflies (Samways and Taylor, 2004). However, increased evaporation and increased aridity in the western parts of the country will decrease annual runoff and river flow. The predicted increases in the frequency and severity of precipitation events across the country will have marked effects on freshwater systems (Knoesen *et al*., 2009).

Some aquatic weeds have been brought under control successfully through the introduction of biological control agents (Coetzee *et al*., 2011). The effect of climate change on biocontrol agents has been poorly investigated. However, variable levels of success in controlling water hyacinth (*Eichhornia crassipes*) have been ascribed to different climatic conditions among invaded sites, pointing to the effect climate may have on biocontrol agents (Coetzee *et al*., 2011). In the case of the water hyacinth and its biocontrol agents, climate change could increase the effectiveness of the agents if conditions become more favourable and enhance the reproductive success of the insects.

Large physiological tolerance ranges of the four alien crayfish species (de Moor, 2002) indicate that these species could potentially spread across large areas and will not be much affected by climate change. This could prove problematic, as freshwater molluscs and crayfish act as intermediate hosts for parasites such as lung fluke and bilharzias, affecting human health (de Kock and Wolmarans, 1998; de Moor, 2002). The potential effects of climate change on other aquatic invaders have not been assessed, and research is required to understand the full range of possible outcomes.

Marine

Current status

Alien marine organisms have arrived in South Africa mainly in the ballast water of ships and attached to ships' hulls as fouling organisms, with fewer than ten introductions associated with mariculture (Mead *et al*., 2011). South Africa's marine habitats support at least 83 alien species and 37 cryptogenic species (species of unknown origin; Mead *et al*., 2011), a drastic increase from the lists of 22 alien and 18 cryptogenic species published in 2009 (Griffiths *et al*., 2009). The lack of knowledge of species distributions and life-history characteristics complicates the task of making informed predictions regarding the potential effects of climate change on indigenous and alien biodiversity. Furthermore, the number of species that are invasive and the potentially environmental and economic impacts of the invaders remains poorly documented. South Africa has 259 estuaries, all of which are extremely vulnerable ecologically. They are being affected by marine and freshwater invasions (Robinson *et al*., 2005), as well as by invasions along riparian zones, which affect the freshwater discharge into estuaries (Richardson and van Wilgen, 2004).

Predictions

There is limited knowledge of indigenous and alien biodiversity along the South African coastline and a lack of data on the species distributions and life-history characteristics of most species. Despite recent advances (e.g. Mead *et al*., 2011), the number of species that are invasive, as well as the potential environmental and economic impacts of the invaders, are not well known. Predictions regarding the responses of marine species to climate change are therefore largely speculative.

The effects of climate change on the marine environment are predicted to be complex and cascading. Between 1985 and 2006, sea surface temperatures of the Agulhas Current have increased 0.7°C per decade, while increases of 1.1°C per decade have been noted at 500 m depth (Rouault *et al*., 2009). Sea surface temperatures are expected to increase by a further 1–3°C before 2050 (Clark, 2006). Sea levels have risen 10–15 mm over the past century and are expected to rise an additional 25 cm by 2050. The frequency and severity of storms will increase; this, in combination with sea level rise, will affect the intertidal zone negatively through coastal erosion, as seen in KwaZulu-Natal in 2007 (Smith *et al*., 2007). Atmospheric [CO_2] heavily influences the marine environment, and the acidity of surface waters will decrease by 0.4 pH units by the end of the century, accompanied by a decline in calcium carbonate saturation levels (Clark, 2006). Increases in ultraviolet radiation are expected to affect photosynthetic rates negatively. The changes are expected to affect the indigenous and alien biota profoundly, either individually or in combination.

Globalization together with climate change will add new trade paths and alter existing ones, across the oceans as well as across land (Galil *et al*., 2007). These will aid the movement of alien species in ballast water, as well as hull-fouling organisms. Furthermore, it has been found that the pollution of harbours by heavy metals affects the indigenous biota negatively and increases the dominance of invasive species (Piola and Johnston, 2008).

Changes in precipitation patterns across the country may result in changes in runoff, and subsequently affect the marine and estuarine environments (Clark *et al*., 2000). The greatest potential effect on South Africa's marine biota due to climate change may be from changes in pressure systems, which are expected to manipulate large-scale oceanographic processes, particularly the upwelling associated with the Benguela region (Clark, 2006). All these climatic alterations will disturb marine environments, making them more susceptible to invasion. Invasive species from lower latitudes are likely to arrive in South African oceanic systems, and warm-water species are likely to become more abundant (Carlton, 2000; Drinkwater *et al*., 2010). Consequently, an overall decline in cold-water indigenous species can be expected.

The response of alien marine organisms to climate change has not been investigated specifically in South Africa, but some predictions can be made by relating the physiological tolerances of a given species to predicted temperature shifts. For example, *Balanus glandula*, a marine invader with a preference for cool, temperate waters, is currently distributed along the western coast, and its range along the south coast is limited by the warmer waters of the Agulhas region. This species could become less abundant with increased ocean temperatures, as it only tolerates temperatures below 17°C (Laird and Griffiths, 2008). The invasion of the European green crab (*Carcinus maenas*) is currently limited to intertidal sites with low wave exposure (Griffiths *et al*., 2009). Changes in storm frequency and severity resulting in increased wave action could induce local extinction of this species. The Mediterranean mussel (*Mytilus galloprovincialis*) affects local mussel diversity negatively by displacing indigenous species on the west coast of South Africa. It seems to prefer cool, temperate conditions and is limited by subtropical environments (Branch and Steffani, 2004), but it is capable of surviving high sea temperatures (Rajagopal *et al*., 2005), and the temperature range for spawning and larval survival is relatively broad (Chícharo and Chicharo, 2000). Wave action has been shown to cause higher mortality in *M. galloprovincialis*, and thus its invasiveness could decline with increasing wave action as a result of climate change (Zardi *et al*., 2008).

Southern Ocean islands

Marion Island, the larger of the two islands in the Prince Edward group, is permanently occupied by a research team, whereas Prince Edward Island is visited only occasionally. The islands have a cool, moist climate, generally very stable, but temperature has increased steadily over the past few centuries and precipitation has declined (Smith and Steenkamp, 1990; Smith, 2002; le Roux and McGeoch, 2008). The Prince Edward Islands have been invaded by numerous alien species, the numbers of which are correlated with the numbers of human visitors during the last two centuries (Chown *et al*., 1998). Because of the much greater number of visitors to Marion, this island has more alien species. Introductions to these islands have been both accidental and intentional. After the impact of the unintentional introduction of the feral house mouse (*Mus musculus domesticus*) on Marion Island was noted, the domestic cat (*Felis catus*) was introduced to alleviate the problem. However, the cats became feral, killing thousands of seabirds, resulting in the active removal of the cats from the island (Chown and Froneman, 2008). The islands have been invaded by at least 13 species of vascular plants (three on Prince Edward) and 18 species of terrestrial invertebrates (one on Prince Edward) (Frenot *et al*., 2005).

Global environmental change, especially rising temperatures, ocean acidification and changes in sea-ice distribution are of immediate conservation concern for the Prince Edward Islands (Chown *et al*., 2012). With climate change, the islands are expected to become warmer and drier. This could open up niches for new alien species to occupy the islands and assist in the spread of established aliens (Frenot *et al*., 2005; Chown *et al*., 2012).

New Threats

Climate change poses a major challenge for the management of alien species in South Africa on many fronts. Besides rearranging the distribution and abundance of species that are already invasive in the country, changing climates will alter the performance of other alien species already in the country but which are not invasive – either because current conditions are suboptimal for them or because they have not had enough time to invade. Dealing with ‘invasion debt’ (the latent expansion of exotic species populations) must be part of a comprehensive strategy for the long-term management of alien species. Nel *et al*. (2004) identified 85 emerging plant invaders – species that currently have little impact on natural or semi-natural ecosystems in South Africa but which are known to have invasive tendencies. Many of these species are likely to flourish under a changing climate, and management and control strategies need to be responsive to these dynamics.

The changing needs of humans will drive the need for new introductions. Interest in biofuels is growing due to global economic trends and the need to reduce dependence on fossil fuels. Although the cultivation of alien plants for the production of biofuels may, in some cases, have clear economic benefits, there are many environmental costs that need to be considered, including the problem that many of the species most suitable for biofuel production are notorious invasive species (Raghu *et al*., 2006; Blanchard *et al*., 2011). Similarly, invasions have resulted and can be expected where plants are cultivated in carbon sequestration projects (Christie and Scholes, 1995; de Wit *et al*., 2001).

Invasion meltdown, the reshuffling and disassembly of communities, may result from novel interactions among species, invasive and indigenous, resulting sometimes in beneficial, but largely detrimental, effects on species or entire ecosystems

(Simberloff and Von Holle, 1999; O'Dowd *et al*., 2003). It is possible that more species indigenous to South Africa may become invasive in parts of the country outside their natural ranges as a result of ongoing human-mediated translocation (Spear and Chown, 2009) or climatic shifts. However, differentiating between unassisted change (i.e. climate change-related only) from directly human-assisted change (i.e. alien invasive species) is a challenge for invasion biology. While the enemy release hypothesis (the ability to thrive in a new environment free of the species' natural enemy) might hold for some species, a recent meta-analysis revealed that not all alien species benefited (Chun *et al*., 2010). Numerous freshwater fish have already spread through inter-basin transfers and now threaten the indigenous biota of these aquatic systems (Macdonald *et al*., 2003). The hadeda ibis (*Bostrychia hagedash* – Macdonald *et al*., 1986b) and the red-billed quelea (*Quelea quelea* – Oschadleus and Underhill, 2006) have expanded their distributional ranges in South Africa as a response to human activity. Dynamic range shifts of several other bird species have been attributed to a combination of land-use change and climate change (Hockey *et al*., 2011). The guttural toad (*Amietophrynus gutturalis*), painted reed frog (*Hyperolius marmoratus*) and African clawed toad (*Xenopus laevis*) have been moved within South Africa and are now considered invasive in the Western Cape (Measey and Davies, 2011). However, distinguishing between climate-induced range expansion and human-assisted translocation is not always straightforward (e.g. Tolley *et al*., 2008; Hockey *et al*., 2011), and is likely to become more complicated in future.

In the face of climate change, indigenous species may have to be translocated for conservation purposes (Mueller and Hellmann, 2008; Richardson *et al*., 2009). Conservation planning must take climate change into account, establishing appropriate corridors between conservation areas, protecting areas of evolutionary significance, expanding transfrontier approaches, practising managed relocation and meeting the challenges posed by invasive species.

Prevention and Management

The prevention and management of biological invasions forms an integral part of South African policy, legislation and government action aimed at protecting the country's biodiversity. Most legislation of direct relevance to the management of biological invasions is incorporated within the Conservation of Agricultural Resources Act (No 43 of 1983), the National Environmental Management: Protected Areas Act (No 57 of 2003) and the National Environmental Management: Biodiversity Act (No 10 of 2004), although many other legal instruments have clauses that can be invoked in this regard (Richardson *et al*., 2003). Management interventions have been implemented both nationally (Working for Water at US\$66 million year^{-1}), provincially (KwaZulu-Natal Invasive Alien Species Programme at US\$13 million year^{-1}) and regionally (e.g. the Invasive Alien Species Strategy for the Greater Cape Floristic Region). Research and capacity-building initiatives include the creation of the DST-NRF Centre of Excellence for Invasion Biology (http://academic.sun.ac.za/cib/), a partnership between government and the tertiary education sector. Biological control of invasive species has proven successful for controlling several invasive species (Coetzee *et al*., 2011; Klein, 2011). Currently, between 1.6 and 2.6% of the total of the Working for Water budget is allocated to biological control, substantially less than is spent on chemical and mechanical control (just under 20% and 80%, respectively) (Le Maitre *et al*., 2011; van Wilgen and de Lange, 2011). The effective implementation of legislation, creating sufficient capacity to undertake the extension and identification work required to prevent new invasions, and the research capacity to keep pace with changing circumstances are all crucial ingredients of an effective strategy to reduce the rates and impacts of biological invasions in the future.

Merging species distribution models (also called niche models) with mechanistic models has potential for predicting the outcomes of complex interactions involving alien species and changing environmental conditions. This has been done for the invasive tree, *Schinus molle*, in South Africa (Richardson *et al*., 2010). Although the overall range of *S. molle* is predicted to shrink in South Africa with predicted climate change, the response of the species is likely to be fundamentally different in different biomes. For example, in areas where it is already highly invasive (notably around Kimberley in the Northern Cape), the considerable propagule pressure that already exists, and which will persist, will facilitate persistence and perhaps even drive further spread, even if climate conditions become marginal. In other areas, the changing flow dynamics of rivers (which create microsites for establishment and facilitate dispersal) are likely to shape invasion dynamics in ways that cannot be accommodated in standard species distribution models (Richardson *et al*., 2010). Ongoing developments in combining mechanistic models with species distribution models could facilitate better predictions.

Overall, the identification of new and emerging invaders, preventing their introduction and managing populations if prevention fails will depend on an informed and aware public, and on science-based policies that take note of the many issues discussed in this chapter. The increased availability of global databases of invasive species is improving our ability to act in preventing further introductions of high-risk species and in calculating and managing the invasion debt. A complete catalogue of all alien species, including those used for agriculture, forestry, horticulture and other purposes, is needed urgently to identify potentially invasive species among already introduced taxa. Proactive early detection and eradication can substantially reduce the costs of control and damage caused by these species (van Wilgen and Richardson, 2009). An important component of mitigation is the effective regulation of the introduction and movement of species. South African legislation to curb such movement is already in place within the National Environmental Management: Biodiversity Act (No 10 of 2004), and the implementation thereof now needs to be addressed. Work will soon start on a National Invasive Species Strategy and Action Plan.

Summary

South African ecosystems are being affected negatively by a wide range of invasive species. Alien invasions and their effects on terrestrial and freshwater systems are currently better understood than marine alien invasions; these are the most prevalent and urgent problems to biodiversity and food security. However, the lack of knowledge and understanding of marine invasions cannot be ignored. It is also clear that numerous potential and ongoing interactions exist between invasive species and aspects of anthropogenic climate change. Our understanding of many of these interactions is conceptual and theoretical, and more illustrative than definitive. None the less, the relationship between climate and invasive species biology is well established, and there is no question that climate change will significantly influence the ecology of biological invasions in this region. For these reasons, several preventive and management efforts could be adapted to help manage changes to system function and services resulting from the interactions between climate change and invasion.

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